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Olfaction in Host Plant Selection of the Soybean Aphid *Aphis Glycines*

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Results from a behavioral study using a four-armed olfactometer (Vet et al, 1983) showed that alate and apterous virginopara of *Aphis glycines* were clearly attracted or arrested by volatiles from *Glycine max*, its secondary host plant, and *Rhamnus davurica*, its primary host plant. The attractiveness of *G. max* was greater than that of *R. davurica*. Chemical analysis indicated that there is some difference in the volatile profiles between these two plant species. The volatiles from two nonhost plant species *Gossypium hirsutrm* and *Cucumis sativa*, which are the most suitable host plants of another aphid A. *gossypii* closely related to *A. glycines*, were found to be neutral. However, the odors of *Luffa cylindrical* and *Cucurbita pepo* significantly repelled the alate virginopara of *A. glycines*. Thus, the olfactory response of *A. glycines* to these host and nonhost plants implies the evolutionary transition of *A. glycines* in host plant specificity.
Blending the odors from nonhost plants *Gossypium hirsutum*, *Luffa cylindrical* and *Cucurbita pepo* with the attractive odor of host plant *G. max* blocked the attractiveness of the latter to the alate virginopara of *A. glycines*. It thus appeared that attractiveness of host plant to aphids can be disrupted by the presence of nonhost plant volatiles which have presumably masked the host plant odor, and the lack of attractiveness of the blended odors is caused by the change in volatile profile.

Key words: *Aphis glycines*, olfaction, plant volatiles, electroantennogram

Aphids fly in the air when the weather is suitable and settle on the host plant. This procedure includes three steps: 1) landing; 2) detecting the plant surface and epithelial structure; 3) piercing the surface with their mouths and checking the food components of the plant. The plant volatiles play a critical role in aphid landing (Klingauf, 1987; Blackman, 1990; Niemeyer, 1990).

The importance of olfaction to aphids' behavior was demonstrated in earlier research about alarming and sexual phenomena (Pettersson, 1970, 1973; Nault and Montgomery, 1977). However, many early researchers indicated that it was by vision, not by olfaction, that aphids searched for host plants (Kennedy et al., 1959; Kennedy, 1986; Xin-JunDe, 1980). Later, researchers indicated that visual orientation could help aphids in the selection of host plants (Moericke, 1969), but the possibility of olfactory attraction couldn't be excluded, even though there was no evidence for demonstrating olfactory attractiveness. Bromley and Anderson (1982) argued that it was wrong to assume that olfaction had no effect on the aphid's host plant selection. Many aphids moved between the primary and secondary host plants which were not related to each other, so it was hard to imagine that without the help of olfactory clues, aphids

habituated to their host plant could land on the exact plants merely by chance. Some studies on aphids' behavior verified that: the plant odors and volatile chemical components were alluring to aphids (Pettersson, 1970,1973; Visser and Taanman, 1987; Nottingham et al., 1991). Chapman and other researchers (1981) lured and trapped a great amount of *Carvoriella aegopodei* with the yellow water solution of *carvone*. The number of trapped aphids decreased when adding the Linalool to the solution. *A. glycines* is a heteroecious aphid. *Rhamnus davurica* is its winter host plant, and *Glycine max*, *G. sp.* and *G. soja Sieb. Et Zucc.* are its summer host plants (Zhang Guang-Xue and Zhong Tie-sen, 1983). Therefore we can conclude that *A. glycines* is strict with host plant selection. It is only harmful to the species of *G. max*. *A. glycines* is the primary economic insect to the species *G. max*, its harmfulness being particularly serious in the northeast areas of China and Inner Mongolia. We used behavioral research and electro-physiological technology to study whether *A. glycines* was attracted by host plant odor when it oriented toward the host plant, and to explain the importance of olfaction and its effect in aphid host plant selection.

Materials and methods

Insect: *A. glycines* were collected on *Rhamnus davurica* in spring from Qinghe County, Beijing, and were cultivated on soybean plants (short early-season variety) indoors. The temperature and illumination were similar to natural conditions.

Plant material: Soybean (short early-season variety, collected from Shangyu county, Zhejiang province). Cotton *Gossypium hirsutum* (86-1), cucumber, *Cucumis sativa*, pumpkin, *Cucurbita pepo* and towel gourd [sponge luffa], *Luffa cylindrica* were collected from the field in Qinghuayuan, suburb of Beijing. The leaves of *R. davurica* were collected from Qinghe County, Beijing. All the collected host plant and non-host plant leaves were picked from the plant and were kept fresh.

Olfactory behavior: A plexiglass four-armed olfactometer was used in the experiment. The equipment was designed as in Pettersson (1970) and Vet (1983)'s experiment. During the experiment a vacuum pump was used to pump the air from the four arms. The airflow volume in each arm was adjusted to 150 ml/min. A stimulating odor source (fresh leaves) was placed in a glass bottle at the end of one of the four arms. The other three arms were controls. Wet filter paper was put in the control glass bottles; the in-flowing air passed through active charcoal. 30 aphids were loaded to the center of the equipment in each experiment. The numbers of aphids in the odor area in each arm were counted every 2 minutes. We counted the numbers continuously in a 20-minute interval to obtain the accumulated number. The experiment was repeated 8 times and we used average number of *A. glycines* as the response. The orientation of the olfactometer was adjusted after two repeats of the experiment and was cleaned with 95% ethanol twice after each experiment. The aphids used had been starved for at least 10 hours before the experiment. The amount of leaves was 8 grams, and they were not cut into pieces. Illumination was provided by four 8W fluorescent lights.

Electroantennogram: the method was according to Visser's experiment (1979). The head and chest of the aphids were cut before the measurement and front legs and one antenna were removed as well. The top of the other antenna was cut and the left antenna was prepared as follows. A reference pole was inserted into the antenna's root and the recording pole (whose diameter was a little larger than that of the antenna) was wound around the top the antenna. The glass pole was made by the vertical capillary puller and its inner diameter was 2 mm. Then,

physiological saline [Kaissling solution: contained glucose (354 mmol/L), KCl (6.4 mmol/L), monopotassium phosphate (20 mmol/L), CaCl (1 mmol/L), MgCl (12 mmol/L), NaCl (12 mmol/L) and KOH (9.6 mmol/L), ph=6.5] was poured in as per Visser (1979). A 0.2 mm diameter Ag-AgCl electrode was inserted into the glass pole and connected with a microelectrode AC-DC amplifier (Nihon Kohden, MEZ-7101), post amplifier (Nanjing electrical physiological instrument factory, FZG-1A), oscillometer (Hameg, HM-203-6) and recorder (Gould, Recorder, 220).

In the whole measurement process, the response of the antenna would become slower. So the response to each odor was described as the value relative to the EAG value of cis-3-hexen-1-ol (1% concentration). The standard compound was used to stimulate the antenna before and after testing with the stimulating compound. All the compounds were soluble in paraffin oil (product of Fluka company) to decrease volatilization. 25μm thixotropic solution was dropped on 6 x 0.5 cm^2 filter paper and the filter paper was put into a drip tube. The end of the drip tube was connected with the stimulating air control equipment and the top was inserted into the hole on the wall of the glass tube with a steady air flow. The flow volume of the attractive air was 80 ml/min and the stimulating time was 0.2 second. The interval between two successive stimulations was over 30 seconds. The continuous airflow was purified with active charcoal and wet by distillation. The air was blown to the aphids' antenna and the experiment was repeated 6 times.

Liu et al. (1989) analyzed soybean volatiles and found that cis-3-hexen-1-ol, 2-hexenal, n-hexanol, 4-hexenyl acetate and 7-octen-4-ol were the major components. So our experiment used the electro-physiological technology to test the olfaction reaction of the aphids' antenna to those components and their analogs. The secondary volatile plant material samples were bought from Roth and Fluka companies (purity ≥ 97%). The chemicals used in the electro-physiological saline were the product of Beijing Chemistry Experiment Factory and the purity was analytical grade.

Results and Discussion

1. Behavior experiment

In the experiment, we selected the host plant of the soybean aphids' relative species, *A. gossypii* as the control. The host plant of *A. gossypii* we selected as controls were: cotton, cucumber, pumpkin and towel gourd. These plants were the non-host plants of the *A. glycines*. The alate and apterous virginopara of *A. glycines*'s olfaction behavior reaction to the volatiles from host plant and non-host plant were carried out in the four-armed olfactometer. The results are shown in Table 1.

The experiment showed that both the alate and apterous virginopara of *A. glycines* had the forward wind taxis to soybean, which was its summer host plant. Alate virginopara of *A. glycines* also had the forward wind taxis to *R. davurica*, its winter host plant and had no wind taxis to the fresh odor of cotton and cucumber, which were its non-host plants. The other two non-host plants, pumpkin and towel gourd had strong repelling effect on alate virginopara of *A. glycines* (Table 1).

Alate virginopara of *A. glycines* had a stronger reaction to its summer host plant, soybean than to its winter host plant, *R. davurica.* This illustrated that different types of *A. glycines* had differences in the olfaction behavior reaction. On the other hand, it showed that there was both similarity and difference in the chemical composition of the volatiles of the soybean and *R. davurica.* The spring-translocated aphids and other kinds of aphids, which moved between soybeans too, were sensitive to the soybean volatiles. The autumn-translocated aphids were sensitive to the volatiles of *R. davurica* there was an adaptation between the aphids and host plants. This result was similar to the result of the experiment on *A. fabae*. Alate virginopara of *A. fabae* had no reaction to the volatiles of its winter host plant, *Euonymus europaeus* (Nottingham et al., 1991).

Table 1. The Olfaction behavioral reaction of *A. glycines* to its host plant and non host plant in the Olfactometer

		Treatment	Control 1	Control 2	Control 3	Action
Alate virginopara of *A. glycines*	Soybean	70.3±27.4	27.6±12.2	27.6±13.9	29.6±12.2	A
	Rhamnus davurica	72.3±15.9	48.9±12.2	49.0±9.2	49.9±7.0	A
	Cotton	25.9±11.6	44.8±20.7	30.9±10.1	40.0±12.8	NS
	Cucumber	46.6±15.9	52.0±15.3	48.8±17.4	55.1±18.0	NS
	Towel gourd	23.4±12.4	53.4±15.3	53.8±9.9	58.9±12.4	R
	Pumpkin	29.6±4.6	61.6±13.9	57.9±13.4	55.3±9.1	R
Apterous virginopara of *A. glycines*	Soybean	72.3±8.5	43.3±8.2	46.3±10.9	46.4±8.6	A

A: attractant, R: repellent, NS: no significant difference in accumulated number of 20 minutes
Experiments repeated 8 times

A. glycines and cotton aphids are related species having a common winter host plant, *R. davurica* (Zhang Guang-Xue and Zhong Tie-sen, 1983; Zhang and Zhong 1990). *A. glycines* and cotton aphid can be hybridized with each other, with the hybrid offspring only surviving on host plants on which the parents thrived. Zhang Guangxue indicated that *A. glycines* evolved from the cotton aphids. The earliest host plant of cotton aphids was the wild pepper *Zanthoxylum simulans*, which was supplanted by *R. davurica* when the latter appeared. After that a branch of cotton aphids shifted to the soybean plant and evolved into today's *A. glycines*. Additionally, after a long period of auxotrophic life cycle on the cucumber, the cotton aphid evolved into an anholocyclic type under the influence of microclimate, and acquired the food preference for cucumber and other kinds of gourd. Based on the results of this experiment, it can be seen that *A. glycines* is more attached to cotton and cucumber than to the towel gourd and pumpkin. The food specificity evolved from millions of years' evolution. *A. glycines'* olfaction reaction to the host plant and non-host plant on the other hand reflected the evolutionary relationship between *A. glycines*, cotton aphids and their host plants.

While the volatiles of soybean alone attracted the aphids, the volatiles of cotton added no obvious repellent effect, and the leaves of towel gourd and pumpkin respectively had repellant effects themselves. But when the leaves of the host plant, soybean, were combined with leaves of non host plants -- cotton, towel gourd and pumpkin -- together, the combined volatiles had

neither obvious attractive nor obvious repellent effect on alate virginopara of *A. glycines* (Table 2). This demonstrated that the attractiveness to alate virginopara of *A. glycines* by volatiles of the host plant could be disrupted by the presence of non-host plant volatiles. This could be due to the repellant effect of the non-host plant volatile, or because its odor masks the effect of the host plant volatile. This phenomenon showed the neutralization of the orientation of the insect's olfaction reaction. The same phenomena were also found among the *A. fabae* and *Brevicoryne brassicae* (Nottingham et al., 1991), and *Leptinotarsa decemlineata* (Thiery and Bisser, 1986, 1987). The attractiveness to *Leptinotarsa decemlineata* by *Solanum tuberosum* could be neutralized by the non-host plant *Lycopersicon hirsutum f. glabratum* or *Brassica oleracea L. var. gemmifera.* Thiery and Visser (1987) explained the cause of this phenomenon as the disguise of the host plant volatiles by blending different volatiles together. The attractive component of *Solanum tuberosum* leaves were mainly made up of widely distributed hexanol, hexanal, and their derivatives. This so-called specificity of green leaves was realized by combining the different components at different concentrations. Certain pure chemical components were added to the composition to change the ratio of that chemical component, so that the forward wind movement of *Leptinotarsa decemlineata* (Visser and Ave, 1978) was disturbed. Meanwhile, adding the volatile of *Lycopersicon hirsurum f. glavratum* would also disturb the forward wind taxis reaction of *Leptinotarsa decemlineata.* Since the volatiles of towel gourd and pumpkin had repellant effects and the volatile of cotton itself had neither attractive nor repellant effect, in this research these two effects may have coexisted.

Table 2. The Olfaction behavioral reaction of the Alate virginopara of *A. glycines* to its host plant and non host plant in the Olfactometer

	Treatment	Control 1	Control 2	Control 3	Action
Soybean	70.3±27.4	27.6±12.2	27.6±13.9	29.6±12.2	A
Cotton	25.9±11.6	44.8±20.7	30.9±10.1	40.0±12.8	NS
Soybean and cotton	50.0±8.9	48.5±14.8	44.4±13.6	48.3±9.6	NS
Towel gourd	23.4±12.4	53.4±15.3	53.8±9.9	58.9±12.4	R
Soybean and towel gourd	52.8±16.5	45.5±9.9	49.6±14.9	63.1±29.5	NS
Pumpkin	29.6±4.6	61.6±13.9	57.9±13.4	55.3±9.1	R
Soybean and pumpkin	48.0±6.4	47.6±14.1	49.3±6.1	53.9±9.9	NS

A: attractant R: repellant NS: no significant difference in accumulated number of 20 minutes
Experiment was repeated 8 times.

2. Electroantennogram Record

With help from the technology of the electroantennogram (EAG), we recorded the EAG reaction of alate virginopara of *A. glycines* to fresh host plant leaves. Figure 1 shows the results. The amount of stimulating leaves was 0.2 gram. The experimental result showed that alate virginopara of *A. glycines* had no reaction to the paraffin solution (control), the relative reaction value to the odor of *R. davurica* was larger than that of the tender leaves of soybean. The unhomogenized plant materials had a stronger effect on alate virginopara of *A. glycines* than homogenized leaves. Alate virginopara of *A. glycines* had no reaction to leaf buds. We could infer that one of the reasons that *A. glycines* did not feed on the leaf buds was because of the difference in its volatile components.

The relative value of alate and apterous virginopara of *A. glycines*'s reaction to the volatile components in soybean plant and other similar plant is shown in Table 3. The EAG value of alate virginopara of *A. glycines* was at the same level as the *Solanum tuberosum* (Visser, 1979*), Psila rosae* (Guerin and Visser, 1980*)* and *Rhynchaenus quercus* (Kozlowski and Visser, 1981). The profile of EAG value of alate virginopara of *A. glycines* against the concentration of cis-3-hexen-1-ol and n-hexanol (fig2a, fig2b) showed that the sense threshold of the antenna's chemical sensor to these two compound reached 10^{-5}-10^{-6} concentrations. So the electro-physiological experiment showed that there existed an olfaction sensor cell in *A. glycines'* antenna to identify the secondary volatile component in the plant. Moreover, the relative value of EAG of the unhomogenized leaves' odor was close to the relative EAG value of the green plant leaves' odor (10^{-2} V/V), though the relative EAG value of the homogenized leaves' odor was similar to that of green leaves' odor (10^{-3} V/V).

Table 3. Relative value of EAG of the alate and apterous virginopara of *A. glycines* to the compounds and other similar materials in the odors of soybean

	alate virginopara of *A. glycines*	apterous virginopara of *A. glycines*
cis-3-hexen-1-ol*	0.20±0.05 mV	0.27±0.08 mV
trans-3-hexen-1-ol	70.9±13.4 mV	89.8±15.1 mV
trans-2-hexenal	170.4±31.0 mV	228.1±87.4 mV
n-hexanol	189.5±28.5 mV	176.8±24.2 mV
1-octen-3-ol	140.2±31.7 mV	197.7±60.9 mV
cis-3-hexenyl acetate	126.5±30.9 mV	132.4±24.6 mV

The concentration of each compound was 1%, n=6

* is the standard compound. The other compounds were described by the relative reaction value of EAG; the test value of that compound was divided by the average value of two test values and was multiplied by 100%.

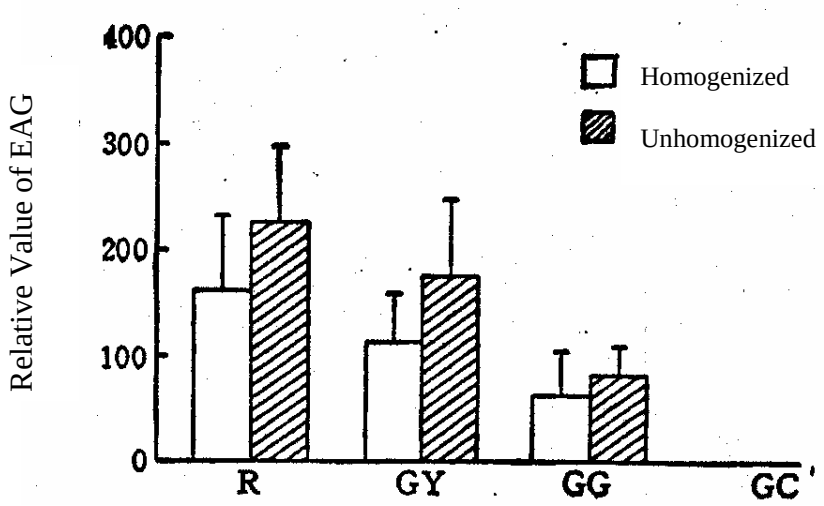

Figure 1. EAG reaction of the alate and apterous virginopara of *A. glycines* to the odors of summer and winter host plants

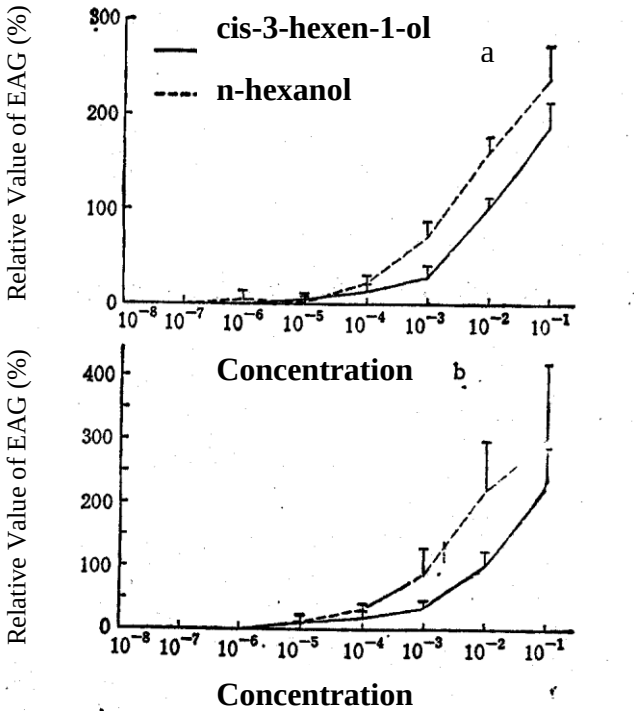

Figure 2. The relative value of EAG of the alate virginopara of *A. glycines* (a) and apterous virginopara of *A. glycines* (b) to the different concentration of cis-3-hexen-1-ol

As seen from their behavioral responses, alate and apterous virginopara *of A. glycines* were attracted by the odors of the host plant. It also showed that *A. glycines* had the positive wind taxis and repelled the non-host plant odor. Additionally, the non-host plant odor could mask the attractiveness of the host plant odor. The electro-physiological experiment proved that the alate and apterous virginopara of *A. glycines*' antenna had an olfaction sensor cell to identify the secondary volatile component in the plant. Those facts strongly demonstrated that the host plant odors of *A. glycines* were very important to the *A. glycines'* selection of the host plant.

It is an important problem to determine whether we can cultivate a mixture of the host plant and non-host plant to eliminate the aphid infestations which are attached to their host plant. According to the report, mixed planting can eliminate the harmful effect of some insects (Stanton, 1983). In the field, the air turbulence can mix the odors of different kinds of plants. The mixed planting can reduce the attractiveness scope of the odor of the host plant. The masking effect on the odor of the non-host plant to the host plant can prevent the host searching of insects.

Though research on the olfaction reaction of the flying aphid is limited to the *Carvoriella aegopodii* (Chapman et al., 1981) and *Phorodon humuli* (Campbell et al., 1990), these field experiments proved that olfaction had an effect during long-distance flying. After landing,

the odors in the neighboring fields are also important. The compounds with the lower volatile rate play a critical role in this situation. So we can conclude that the secondary volatile component in the *A. glycines*' winter host plant, *R, davurica* and summer host plants, soybean has a very important effect on the movement of *A. glycines* between the host plants.

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